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A REVIEW OF THE GENUS *KROMBEINIUS* (HYMENOPTERA: PERILAMPIDAE) WITH A REEXAMINATION OF GENERIC LIMITS AND PHYLOGENETIC RELATIONSHIPS AND THE DESCRIPTIONS OF TWO NEW SPECIES

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Abstract.—The world species of *Krombeinius* are reviewed and two new species are described, *K. taiwanensis* from Taiwan and *K. srilanka* from Sri Lanka. A cladistic analysis strongly supports the monophyly of *Krombeinius* and *Euperilampus* and provides a phylogenetic hypothesis for the relationships of the species of *Krombeinius*.

In my earlier contributions to the systematics of *Krombeinius* and *Euperilampus* (Darling, 1983a, b) I noted that the genus *Krombeinius* was characterized by the absence of the synapomorphies of *Euperilampus*, by symplesiomorphy. As a solution, I proposed the unique configuration of the labrum as an autapomorphy of *Krombeinius*, based only on the type species *K. eumenidarum*. The recent description of a new species of *Krombeinius* from the Ethiopian region (Rasplus, 1987) and the discovery of additional undescribed Oriental species in collections have provided the opportunity to test this prediction. I have now been able to examine the labrum in two additional species of *Krombeinius* and the morphology is consistent with that hypothesis of monophyly. This additional material also provided the impetus to review the world species of *Krombeinius* and to investigate their phylogenetic relationships.

The referral of these new species to the genus *Krombeinius* was initially problematic and required a revised generic concept. The description and diagnosis of the genus are herein modified to a significant degree. The previous diagnosis was effectively a phenetic characterization which can now be replaced with a synapomorphy scheme. The result is a taxon based on a hypothesis of common ancestry that includes phenetically rather dissimilar species due to the differential retention of, and reversal to, primitive features.

Abbreviations used in the text: F1–7, funicular segments; MSC, length of mesoscutum along midline; OOL, length of ocular-ocellar line; PN, length of pronotum along midline; POL, length of posterior ocellar line; SC, length of scutellum along midline; T2–8, metasomal tergites 2–8. Figures are referred to by the convention: Fig., for figures in this paper and fig., for figures in previous publications. Sculpture types follow Eady (1968).

Krombeinius Bouček

Krombeinius Bouček, 1978:302, figs. 1, 2 [original description, key]; Darling, 1983a: 308, figs. 1, 2, 3, 6–17 [diagnosis, description, phylogenetic relationships]; Darling, 1983b:34, fig. 77 [phylogenetic relationships].

Type species: *Krombeinius eumenidarum* Bouček, 1978:302, fig. 1. [original designation]

Diagnosis. Moderately large (3 to 6 mm) and robust perilampids, black in color without metallic reflections (habitus drawing in Darling, 1983a), differentiated from other perilampid genera by the following combination of characters (apomorphies in bold face): marginal vein of forewing longer than postmarginal vein (Figs. 8, 14); **labrum with a central stalk,** lacking aboral digits (Fig. 4); **third metasomal tergite massive, much larger than second** (Darling, 1983a, fig. 1); and malar sulcus obliterated by oblique costae (Figs. 1, 2).

Description. Head: subequal in width to pronotum, in dorsal view transverse; supraclypeal area smoothly convex, without horn or ridge; scrobal cavity deep, extended to lower ocular line or to middle of clypeus; lower edge of antennal torulae above lower ocular line; clypeus and supraclypeal area separated by distinct suture or by faint line; inner orbits carinate and in some species developed as prominent scrobal walls, smooth or with distinct costae; frontal carina separating the median and posterior ocelli; malar sulcus absent; malar region with oblique costae; OOL/POL diagnostic; labiomaxillary complex short, maxillary palp 4-segmented, labial palp 3-segmented; labrum with a narrow central stalk, expanded distally with 7–10 short digits, each with a tapered seta, and with paired sessile setae not associated with digits.

Mesosoma: dorsum of pronotum smoothly convex, without transverse elevations; pronotum variable in size and shape; mesothoracic spiracle located between pronotum and sidelobe of mesoscutum; prepectus fused to the pronotum, width variable relative to adjacent pronotum, with many or a single fovea; notauli distinct and complete; scutellum vaulted, jutting over propodeum and base of metasoma; apex of scutellum acuminate, truncate or with a distinct spine; propodeum with median area foveate, or with a short median ridge, submedian areas with weak transverse rugae or aciculate; basitarsomere not conspicuously lengthened. Forewing with marginal vein longer than postmarginal, postmarginal vein long, about 2–3 times length of stigmal vein, stigmal vein making either 90° or oblique angle with marginal vein.

Metasoma: petiole short, transverse, the tergum forming a ridge along anterior face of gaster, sternum shifted posteriorly; T2 and T3 fused, covering most of dorsum; T3 massive and convex, about twice length of T2 along midline, length about equal to maximum width; ovipositor ventral, not upturned, sheaths not distinctly exserted; male genitalia with distinct parameres.

KEY TO THE SPECIES OF *KROMBEINIUS*

1. Inner orbits with strong costae, extended from posterior ocelli to clypeus (Darling, 1983a, figs. 8, 9, 16, 17); pronotum, in lateral view, with distinct callus, giving the impression of bumpy shoulders (Darling, 1983a, fig. 1) 2

1′. Inner orbits smooth, without strong costae (Figs. 1, 2, 10, 11); pronotum without distinct callus (Fig. 13), if callus weakly developed (Fig. 6) then head, in lateral view, without inner orbits developed as prominent scrobal walls (Fig. 2) 3

2(1). Apex of scutellum with prominent spine (Darling, 1983a, figs. 1, 15) [Philippines] .... *K. saunion*

2′(1). Apex of scutellum truncate, not produced as a prominent spine (Figs. 5, 6, 12, 13) [Southern India, Sri Lanka] .... *K. eumenidarum*

3(1′). Third metasomal tergite (T3) finely and densely punctulate; malar region with very weak and short costae (Figs. 10, 11) [Sri Lanka] .... *K. srilanka,* n. sp.
3′(1′). Third metasomal tergite (T3) smooth, without impressed surface sculpture; malar region with distinct oblique costae (Figs. 1, 2) 4
4(3′). Prepectus with single fovea (Bouček, 1978, fig. 2); propodeum and metanotum subequal in length [Malaysia, Sarawak] .... *K. megalaspis*
4′(3′). Prepectus with many foveae (Fig. 7); propodeum about twice length of metanotum 5
5(4′). Head, in lateral view, broad, inner orbits developed as prominent scrobal walls (as in Fig. 10); scutellum, in lateral view, evenly convex, gradually tapered toward apex (Rasplus, 1987, fig. 1) [West Africa] .... *K. lerouxi*
5′(4′). Head, in lateral view, narrow, inner orbits not developed as prominent scrobal walls (Fig. 2); scutellum, in lateral view, vaulted, not gradually tapered toward apex (Fig. 6) [Taiwan] .... *K. taiwanensis,* n. sp.

SYNOPSIS OF THE WORLD SPECIES OF *KROMBEINIUS*

Krombeinius eumenidarum Bouček
Fig. 17

Krombeinius eumenidarum Bouček, 1978:302, fig. 1; Darling, 1983a, figs. 2, 3, 6–9 [male genitalia, labrum, phylogenetic relationships].

Distribution. Sri Lanka, India.

Diagnosis. This species can be distinguished by the combination of costate inner orbits and truncate scutellum, not produced as an elongate spine as in *K. saunion* (Darling, 1983a, fig. 15). This species can be further distinguished from its sympatric congener, *K. srilanka,* by the more massive scrobal walls with distinct costae (Darling, 1983a, fig. 17; cf. Fig. 10) and much larger pronotum, in dorsal view one-third length of mesoscutum *versus* one-fifth (Darling, 1983a, fig. 15; cf. Fig. 12) and smaller prepectus, in lateral view about one-third width of adjacent pronotum *versus* about one-half (Darling, 1983a, fig. 1; cf. Fig. 13).

Host. This species is a primary parasitoid of *Paraleptomenes mephitis* (Cameron) [Vespidae: Eumeninae] (see Krombein, 1978).

Krombeinius megalaspis (Cameron)

Perilampus megalaspis Cameron, 1912:63; Bouček, 1978, fig. 2 [lectotype designation, n. comb.]; Darling, 1983a, figs. 10–13 [phylogenetic relationships].

Distribution. Malaysia, Sarawak.

Diagnosis. Only this species and *K. lerouxi* have the inner orbits smooth but still developed as prominent scrobal walls. These species may be distinguished by the relative sizes of the propodeum and metanotum; subequal in length in *K. megalaspis* and the metanotum is only about one-half length of propodeum in *K. lerouxi.* In addition, the pronotum in lateral view is regularily convex in *K. megalaspis,* without the raised callus which gives the suggestion of bumpy shoulders in specimens of *K. lerouxi* (as in Fig. 6).

Notes. In my earlier discussion of the genus I noted that this species was problematic in many regards and that a revised classification might necessitate a new monobasic genus. The cladogram (Fig. 19) suggests that this species may be the sister group to the other species of the genus. Known only from the type material.

Krombeinius saunion Darling

Krombeinius saunion Darling, 1983a:313, figs. 1, 14–17 [phylogenetic relationships].

Distribution. Philippines, Mindanao.

Diagnosis. This is the only species of the genus with the apex of scutellum produced as a prominent spine. In other characters the species is quite similar to *K. eumenidarum* (additional distinguishing features are presented in Darling, 1983a).

Notes. The name of this species was inadvertently spelled in two ways in the original publication. Following the Principle of the First Reviser [ICZN 1983, Articles 24 and 32 (b)(i)], the above name is here chosen as the correct original spelling. Known only from the holotype.

Krombeinius lerouxi Rasplus
Fig. 15

Krombeinius lerouxi Rasplus, 1987:9, figs. 1–3.

Distribution. West Africa (Ivory Coast, Cameroon).

Diagnosis. This species and *K. megalaspis* are the only species in which the stigmal vein makes an oblique angle with the marginal vein (Rasplus, 1987, fig. 3). In all other species this angle is approximately 90° (Figs. 8, 14). These two species can be distinguished by the relative sizes of the propodeum and metanotum (see "Diagnosis" of *K. megalaspis*). The male of *K. lerouxi* has infumate wings in the region surrounding the sitgmal vein and a distinctive pattern of punctures on the surface of the male scape (Fig. 15).

Redescription. Female: Length, about 6 mm. Black, except tegula and mandible reddish-brown, foretibial spur and tarsi yellow; wings hyaline, veins darkened.

Head (Rasplus 1987, figs. 1, 2): wider than pronotum, in dorsal view transverse, width : length = 1.92; in frontal view transverse, width : height = 1.16; maximum width of scrobe 0.52 head width; frontal carina extended below lower ocular line, convergent on clypeus; length of malar space 0.22 eye height; OOL 0.95 POL; inner orbits smooth and shining, developed as prominent scrobal walls; outer orbits costate, convergent on clypeus (Fig. 1); scrobal cavity deep and broad, delimited by frontal carina, extended to lower ocular line; clypeus transverse, width : height = 1.50, polished and sparsely covered with setae, longer and denser along margin; clypeus delimited by weak sutures and with raised median callus, upper margin indicated by faint line, lower margin strongly emarginate; tentorial pits indistinct; supraclypeal area glabrous, height 0.52 clypeus height, convex along midline, laterad with distinct channels for reception of antennae; ocular-ocellar region smooth and shining without costae radiating from ocelli; vertex with strong costae at posterior margin. Labrum with 8–10 very short subsessile digits and strongly excised medially (inverted Y-shape, much more strongly excised than in *K. taiwanensis,* Fig. 4 and *K. eumenidarum,* Darling, 1983a, fig. 3). Antenna: scape narrowly linear, length about 7.3 maximum width; pedicel and funicular segments (F1–F7) subequal in length (17 *versus* 14, 14, 15, 14, 14, 11, 13); pedicel 0.21 scape length; annellus 0.32 length of F1; F1–F7 transverse, wider than long; clava 0.38 length of funicle.

Mesosoma (Rasplus, 1987, fig. 1): pronotum massive, PN:MSC = 0.26, as in *Perilampus,* lateral pronotum rounded, with only a slight suggestion of bumpy shoulders; scutellum acuminate, SC:MSC = 1.23; dorsum of pronotum, midlobe of mesoscutum, and scutellum punctate-reticulate, coalesced to form weak transverse costulae medially; sidelobes of mesoscutum smooth along notauli, laterally punctate; scutellum in lateral view not strongly convex; underside of scutellum smooth, with shallow convergent grooves; median area of propodeum foveate, about twice as long as metanotum (49:28), submedian areas delimited by lateral ridges, with transverse costulae, callus not raised, on the same plane as submedian areas, coriarious; width of prepectus 0.49 width of adjacent pronotum, with about 8 foveae, sculpture differentiated from adjacent pronotum by narrow glabrous area; axilla punctate-reticulate above, smooth below, without distinct costae; axillula triangular and not extended towards apex of scutellum as fingerlike lobe, without distinct crenulae. Forewing venation (Rasplus, 1987, fig. 3): submarginal vein 2.6 marginal vein, postmarginal 0.57 marginal, stigmal 0.26 marginal, stigmal 0.46 postmarginal, stigmal vein making oblique angle (125°) with marginal vein, stigma expanded below, with 3 or 4 sensilla.

Metasoma: T2 smoothly concave with sparse setae concentrated at posterolateral margin, without punctures, laterotergite glabrous; border between T2 and T3 indicated by sinuous suture; dorsal surface of T3 evenly covered with short setae except along T2 border and along margins of tergite, without distinct punctures; ovipositor not examined.

Male: Differs from female only in following regards: forewing infuscate in region surrounding stigmal vein; clypeus with many more setae; scape, in frontal view, expanded apically with punctures distributed in a distinct V-shaped pattern (Fig. 15).

Notes. This redescription is based on the holotype female (Museum National d'Histoire Naturelle, Paris) and a recently collected topotypic male specimen. The host of this species is unknown but paratypes were reared from tree branches. As noted by Rasplus (1987), it is certainly possible that the branches contained nests of eumenine vespids.

Krombeinius taiwanensis, new species
Figs. 1–8

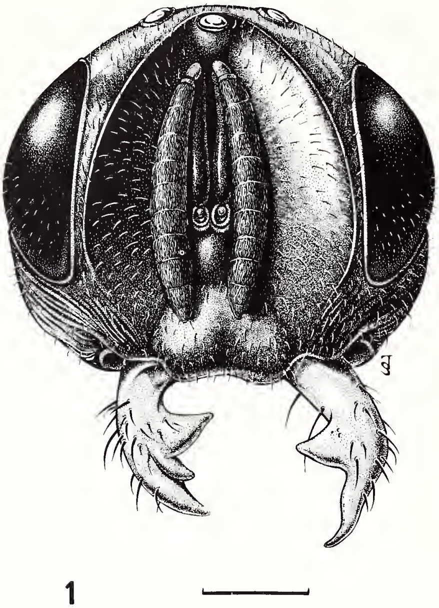
Type locality. Taiwan.

Type material. "Kurario [?] Formosa Gressitt [collector]," handwritten; Slide #595–596 D. Chris Darling, labrum, labiomaxillary complex; Holotype ♀ *Krombeinius taiwanensis* D. Chris Darling '88. The specimen was remounted on cards after dissection of the mouthparts. The body is on the top card with the head detached. The lower card has the original paper point, with midlegs still attached, and the antennae; the specimen is otherwise in excellent condition. The mouthparts are slide-mounted in Canada Balsam.

Type repository. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

Etymology. The specific epithet is a reference to the type locality.

Diagnosis. This species can be recognized immediately as the only member of the genus without the inner orbits developed as prominent scrobal walls, the head in



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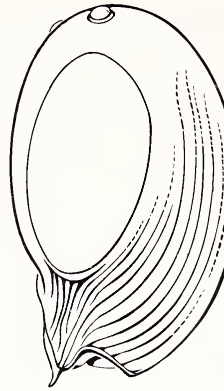

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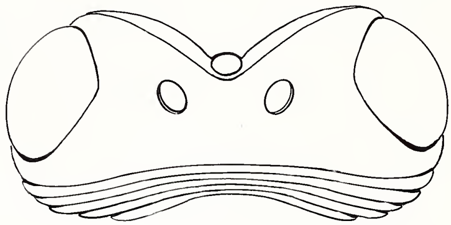

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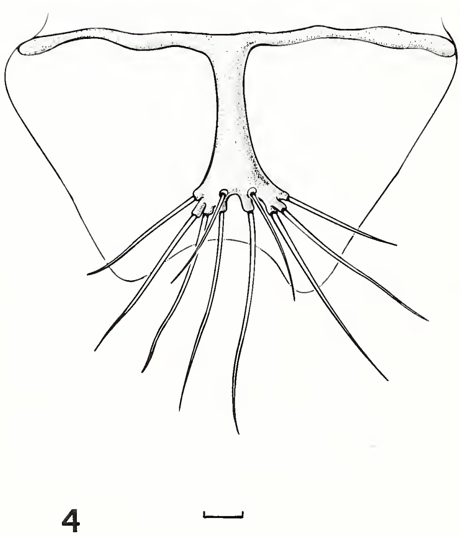

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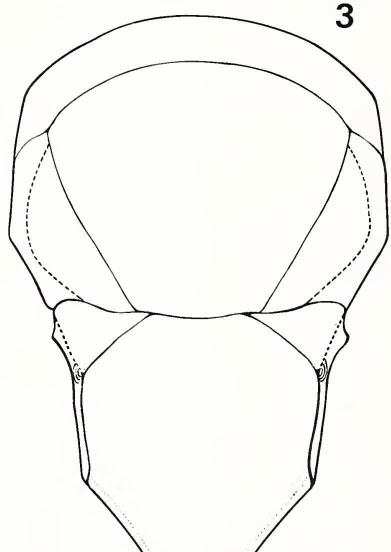

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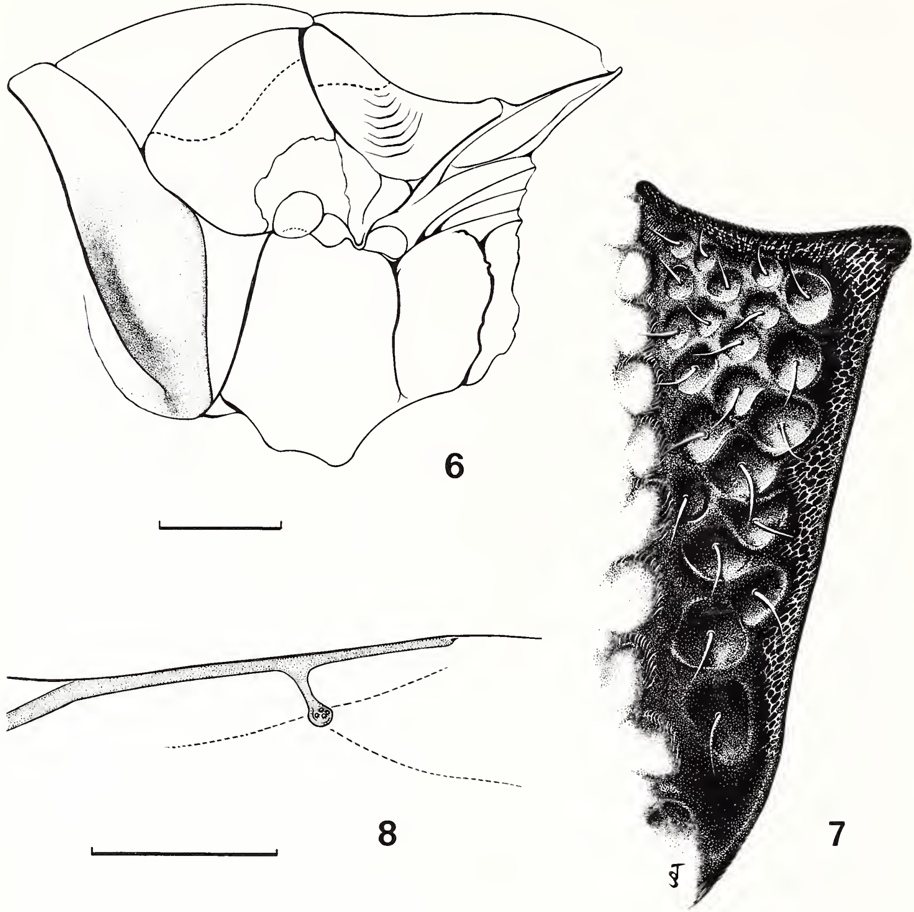
Figs. 1–5. *Krombeinius taiwanensis,* new species. 1. Head, frontal. 2. Head, lateral. 3. Head, dorsal. 4. Labrum and epipharynx. 5. Mesosoma, dorsal; dashed line indicates extent of smooth areas along notauli and on axillae. Figs. 1–3, 5 drawn to same scale, scale line 0.5 mm; Fig. 4, scale line 0.05 mm.

lateral view is narrowly convex (Fig. 2; cf. Fig. 10 and figs. 9, 13, and 17 in Darling, 1983a). This species and *K. srilanka* share a number of similarities. In both species, the prepectus is much wider than in all other species, greater than one-half the width of the adjacent pronotum *versus* approximately 0.45 in all other species (Fig. 6; cf. fig. 1 in Darling, 1983a and figs. 1, 2 in Bouček, 1978) and the pronotum is narrow in dorsal view, 0.2 the length of the mesoscutum *versus* 0.30–0.35 (Fig. 5; cf. figs. 7, 11, and 15 in Darling, 1983a). The strong costae in the malar region will distinguish these two species (Fig. 2; cf. Fig. 10).

Description. Female: Length, 5 mm. Black, except tegula and flagellum brown, mandible reddish-brown, apex of foretibia and spur, and tarsi yellow; wings hyaline, veins darkened.

Head (Figs. 1–3): wider than pronotum, in dorsal view transverse, width : length = 1.97; in frontal view transverse, width : height = 1.12; maximum width of scrobe 0.64 head width; frontal carina extended below lower ocular line; length of malar space 0.31 eye height; OOL 0.94 POL; inner orbits smooth and shining, not developed as prominent scrobal walls; outer orbits with costae convergent on clypeus (Fig. 1); scrobal cavity deep and broad, delimited by frontal carina, extended to lower ocular line; clypeus transverse, width : height = 1.40, polished and sparsely covered with setae, longer and denser along margin; clypeus delimited by weak sutures and with raised median callus, upper margin indicated by faint line, lower margin strongly emarginate (Fig. 1); tentorial pits indistinct; supraclypeal area glabrous, height 0.68 clypeus height, convex along midline, laterad with distinct channels for reception of antennae; lower edge of antennal torulae above lower ocular line; ocular-ocellar region smooth and shining without costae radiating from ocelli (Fig. 3); vertex with strong costae at posterior margin. Labrum (Fig. 4): with 8 very short subsessile digits and not strongly excised medially (cf. *K. eumenidarum,* Darling 1983a, fig. 3). Antenna: scape narrowly linear, length about 8.5 maximum width; pedicel and funicular segments (F1–F7) subequal in length (17 *versus* 12, 12, 14, 13, 14, 14, 12); pedicel 0.26 scape length; annellus 0.41 length of F1; F1–F7 transverse, wider than long; clava 0.38 length of funicle.

Mesosoma (Figs. 5–7): pronotum not massive, PN:MSC = 0.19, as in *Perilampus,* lateral pronotum convex, with only slight suggestion of bumpy shoulders, much less distinct than in *K. eumenidarum*; scutellum truncate (Fig. 5), SC:MSC = 1.12; dorsum of pronotum, midlobe of mesoscutum, and scutellum punctate-reticulate; sidelobes of mesoscutum smooth along notauli, laterally punctate-reticulate; scutellum in lateral view strongly convex, apex high, subvertical (Fig. 6); underside of scutellum smooth, with shallow convergent grooves; median area of propodeum with deep crenulate groove along anterior margin and median ridge about twice as long as metanotum (49:28), submedian areas distinctly delimited by median and lateral ridges, with transverse costulae, callus reticulate-rugose; width of prepectus 0.60 width of adjacent pronotum (Fig. 6), with about 20 foveae (Fig. 7), sculpture undifferentiated from adjacent pronotum; axilla punctate-reticulate above, costulate below; axillula large and distinctly separated from scutellum and extended towards apex of scutellum as fingerlike lobe (Fig. 6), smooth except for weak crenulae ventrad. Forewing venation (Fig. 8): submarginal vein 2.9 marginal vein, postmarginal 0.62 marginal, stigmal 0.26 marginal, stigmal 0.43 postmarginal, stigmal vein making slightly oblique angle with marginal vein, stigma rounded with 4 sensilla.



Figs. 6–8. *Krombeinius taiwanensis,* new species. 6. Mesosoma, lateral view. 7. Prepectus. 8. Forewing venation. Scale lines, 0.5 mm.

Metasoma: T2 smoothly concave with sparse setae, without punctures, laterotergite glabrous; border between T2 and T3 indicated by sinuous suture; T3 smooth and shining, evenly covered with short setae except along T2 border and along margins of tergite, with distinct but small punctures laterad; ovipositor not examined.

Male: Unknown.

Krombeinius srilanka, new species
Figs. 9–14, 16

Type locality. Trincomalee, Sri Lanka.

Type material. "Sri Lanka: Tri. Dist. Trincomalee, China Bay Ridge Bungalow 0-100′," "Adult eclosed 2 Aug 1978 K. V. Krombein," "Host: *Paraleptomenes mephitis*

(Sauss.)," "Holotype ♂ *Krombeinius srilanka* D. Chris Darling '88." The specimen is point-mounted and in excellent condition.

Type repository. United States National Museum, Washington, DC, U.S.A.

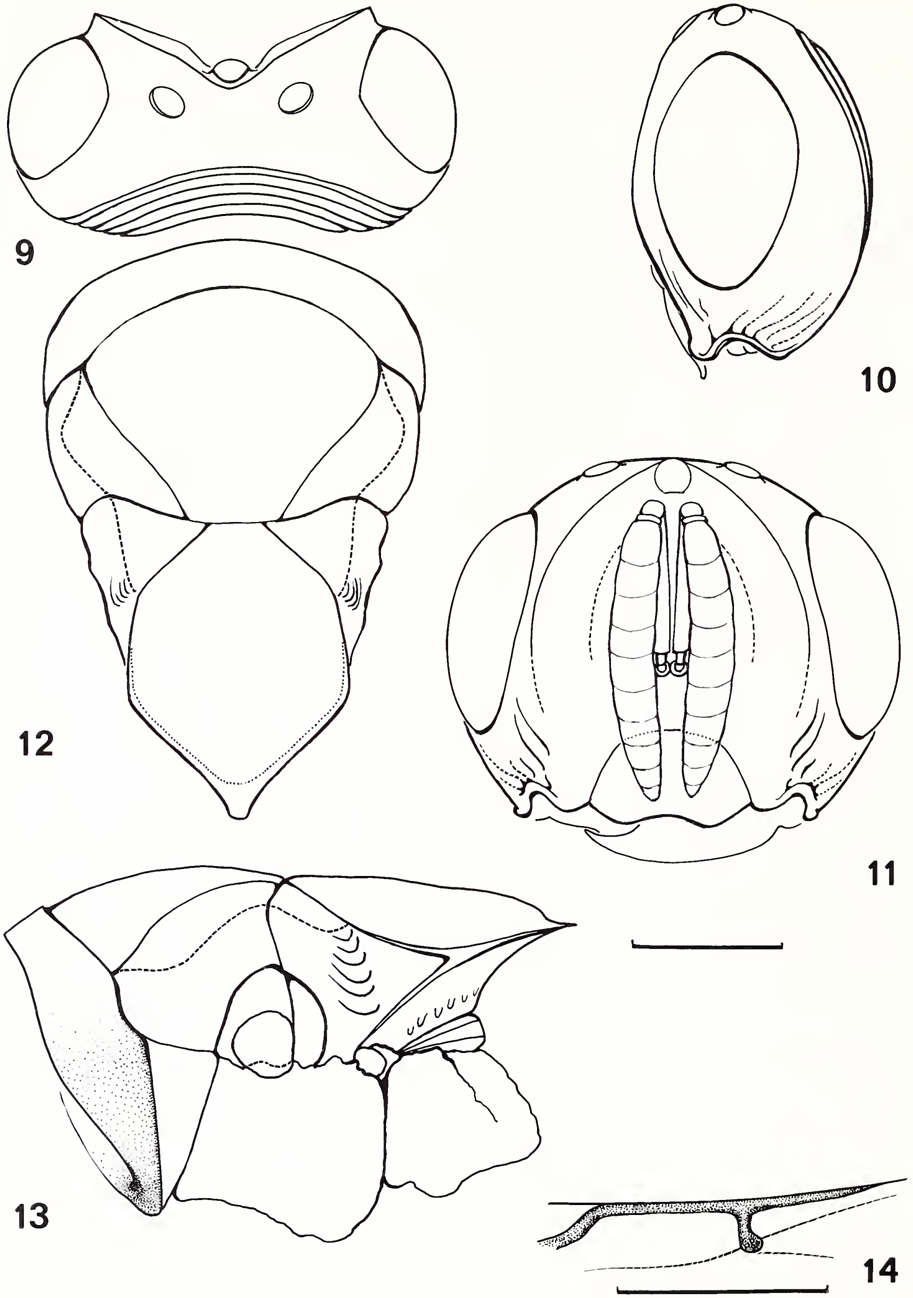
Etymology. The specific epithet is a noun in apposition, a reference to the type locality.

Diagnosis. This is the only species in the genus with distinct sculpture covering the majority of the surface of either T2 or T3; both sclerites are sculptured in this species. In addition, *K. srilanka* differs from all other species by having fewer and weaker costae in the malar region (Fig. 10; cf. Fig. 2) and having the lateral ocelli situated much closer to the eyes than the anterior ocellus, OOL about one-half POL *versus* OOL = POL (Fig. 9; cf. Fig. 3). Additional characters to distinguish this species and its sympatric congener, *K. eumenidarum,* include smooth inner orbits *versus* costate (Fig. 10; cf. fig. 9 in Darling, 1983b) and the pattern and distribution of punctures on the male scape (Fig. 16; cf. Fig. 17). See also "Diagnosis" of *K. eumenidarum.*

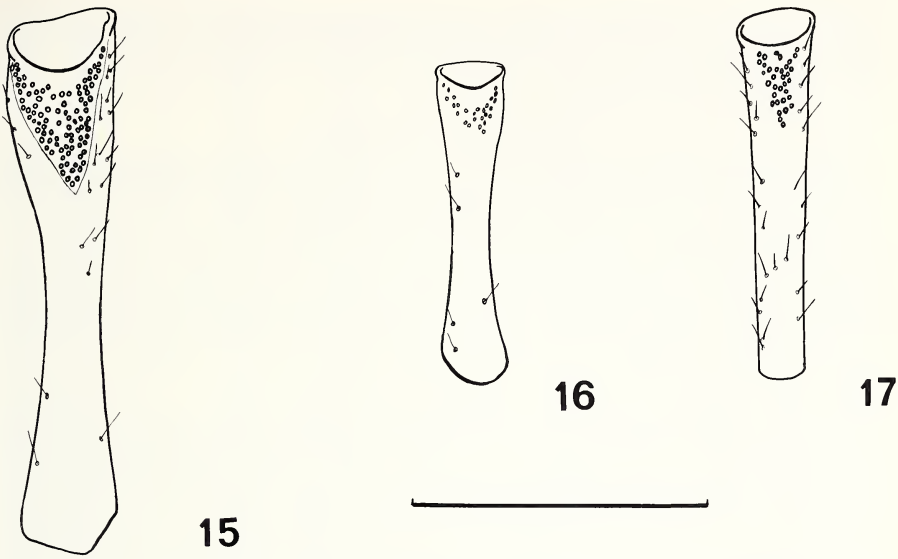
Description. Male: Length, 3.5 mm. Black, except flagellum brown, mandible reddish-brown, tegula, apex of foretibia and spur, and tarsi yellow; wings hyaline, veins darkened.

Head (Figs. 9–11): wider than pronotum, in dorsal view transverse, width : length = 2.0; in frontal view transverse, width : height = 1.15; maximum width of scrobe 0.63 head width; frontal carina not reaching lower ocular line; length of malar space 0.20 eye height; posterior ocelli closer to eyes than in other species (Fig. 9), OOL 0.51 POL; inner orbits smooth and shining, developed as low scrobal walls (Fig. 10); outer orbits smooth without distinct costae (Figs. 10–11); scrobal cavity deep and narrow, not delimited by frontal carina, extended to lower ocular line; region between frontal carina and scrobal declivity with long and dense white setae; clypeus transverse, width : height = 1.74, polished and sparsely covered with setae, longer and denser along margin; clypeus delimited by weak sutures and without median callus, upper margin indicated by distinct suture, lower margin strongly emarginate (Fig. 11); tentorial pits indistinct; supraclypeal area glabrous, height 0.65 clypeus height, convex along midline, without distinct channels for reception of antennae; ocular-ocellar region smooth and shining without costae radiating from ocelli (Fig. 9); vertex with strong costae at posterior margin. Labrum not examined. Antenna: scape length about 4.8 maximum width; flagellum long, reaching anterior margin of clypeus; pedicel and funicular segments (F1–F7) subequal in length (10 *versus* 14, 11, 12, 13, 13, 12, 11); pedicel 0.24 scape length; annellus small, 0.21 length of F1; F1–F7 transverse, wider than long; clava 0.24 length of funicle; scape, in frontal view, expanded only slightly apically with punctures distributed as in Fig. 16.

Mesosoma (Figs. 12, 13): pronotum not massive, PN:MSC = 0.20, lateral pronotum flat, without any suggestion of bumpy shoulders; scutellum truncate, with crenulate margin but not completely delimited by distinct carina, SC:MSC = 1.23; dorsum of pronotum, midlobe of mesoscutum, and scutellum punctate-reticulate, punctures not coalesced to form transverse costulae medially; sidelobes of mesoscutum smooth along notauli, laterally punctate; scutellum in lateral view convex (Fig. 13); underside of scutellum roughened, without convergent grooves; propodeum with distinct median ridge, submedian areas with transverse costae, medially about twice as long as metanotum (35:17), submedian areas delimited by median and lateral ridges, with



Figs. 9–14. *Krombeinius srilanka,* new species. 9. Head, dorsal. 10. Head, lateral. 11. Head, frontal. 12. Mesosoma, dorsal; dashed line indicates extent of smooth areas along notauli and on axillae. 13. Mesosoma, lateral. 14. Forewing venation. Figs. 9–13 drawn to same scale, scale line 0.5 mm; Fig. 14, scale line 0.05 mm.



Figs. 15–17. *Krombeinius* species, male scapes. 15. *K. lerouxi*. 16. *K. srilanka*. 17. *K. eumenidarum*. Scale line, 0.5 mm.

transverse costulae, callus large and raised, reticulate-rugose; width of prepectus 0.55 width of adjacent pronotum (Fig. 13), with about 16 foveae, differentiated from adjacent pronotum by narrow glabrous area; axilla punctate-reticulate above, costulate below; axillula triangular, not extended towards apex of scutellum as fingerlike lobe, smooth except for weak crenulae ventrad. Forewing venation (Fig. 14): submarginal vein 3.4 marginal vein, postmarginal 0.74 marginal, stigmal 0.24 marginal, stigmal 0.33 postmarginal, stigmal vein making slightly oblique angle with marginal vein, stigma rounded with 4 sensilla.

Metasoma: T2 concave with distinct groove along midline, aciculate with setae only at the posterolateral margin, without punctures; basal fovea distinct and transverse; laterotergite glabrous; border between T2 and T3 indicated by sinuous suture; T3 finely reticulate-coriarious, evenly covered with long setae except along T2 border and along margins of tergite.

Female: Unknown.

Host. This species is a primary parasitoid of *Paraleptomenes mephitis* (Cameron) [Vespidae: Eumeninae].

Notes. It is somewhat disconcerting that this species is sympatric with *K. eumenidarum* and also attacks the same species of potter wasp. Initially, consideration was given to broadening the concept of *K. eumenidarum* to include this specimen. A male specimen was available for comparison (India, Kerala, length 4.2 mm). As discussed in the diagnosis, these species are quite different in morphology; furthermore, the phylogenetic analysis suggests that these sympatric species are only distantly related within the genus. The number and distribution of punctures on the male scape supports the hypothesis that two distinct species are involved. The male scape has proven to be of considerable value in distinguishing species in other perilampid genera (e.g., *Euperilampus,* Darling, 1983b) and the hypothesized sister group of the Perilampidae, the Chrysolampinae (Darling, 1986).

PHYLOGENETIC ANALYSIS

A phylogenetic analysis was conducted to refine the previous cladogram presented for the derived elements of the Perilampidae (Darling, 1983b). The monophyly of *Krombeinius* + *Euperilampus* needed to be reconsidered in light of the unique combinations of characters exhibited by *K. taiwanensis* and *K. srilanka.* The genera were previously related on the basis of four synapomorphies, all of which are now suspect. The second goal was to test the monophyly of the traditional genera, *Euperilampus* and *Krombeinius.* Finally, intrageneric relationships were investigated for the six species of *Krombeinius.*

Character polarity was initially determined using the *Perilampus hyalinus* species group as the outgroup, based on a sister group relationship between this species group and *Euperilampus* + *Krombeinius* (Darling, 1983b). The *Euperilampus scutellatus* species group was included to represent the groundplan characters for this genus. Twenty-three characters were coded for the eight taxa (Table 1). Parsimony analyses were conducted using the PAUP program (David Swofford, Illinois Natural History Survey). The small number of taxa allowed the use of the ALLTREES option, guaranteeing the shortest tree(s), and the BBSAVE = x option, to determine how many trees were only slightly longer than the shortest possible tree. The UNORDERED option was used to investigate possible codings for multistate characters and the DELCHAR option was used to investigate the influence of individual characters on the shortest trees. Strict consensus trees were constructed using the CONTREE program in the PAUP package.

Character 1. The sculpture of the inner orbits exhibits diverse configurations in the Perilampidae. In *Burksilampus, Steffanolampus,* and all plesiomorphic species groups of *Perilampus* the inner orbits are smooth or impunctate. Distinct raised rugae or costae are found only in the *Perilampus hyalinus* group, *Euperilampus,* and *Krombeinius.* However, smooth or impunctate sculpture is also found in all three groups. I previously interpreted costate inner orbits as a synapomorphy of *Euperilampus* + *Krombeinius* (Darling, 1983b, character 13). An equally parsimonious interpretation is that this character is synapomorphic at the level of *P. hyalinus* group + (*Euperilampus* + *Krombeinius*). I have coded costate inner orbits as plesiomorphic (state 0) and regard smooth or impunctate inner orbits as derived (state 1) in *Krombeinius*; a similar reversal to a phenotypically plesiomorphic condition is evident in *Euperilampus* (Darling, 1983b). The cladogram (Fig. 19) suggests that the common ancestor of *Krombeinius* species had smooth inner orbits and that the costate inner orbits of *K. eumenidarum* + *K. saunion* and *Euperilampus* species are a result of convergence, not the retention of an ancestral character.

Character 2. In the initial analysis multiple characters were coded that dealt with the configuration of the pronotum and prepectus. In my earlier study (Darling, 1983b) I recognized two characters, width of prepectus (character 3) and size of pronotum in dorsal view (character 12). In this study I initially added a third character, the shape of the pronotum in dorsal view. In each analysis homoplasy was present in each of the three characters and the extra steps in each character occurred at the

Table 1. Character states for 23 characters and 8 taxa included in the cladistic analysis (0 = ancestral state; 1, 2, 3 = derived states; ? = missing data). See text for discussion of character polarity and transformation series.

Taxon	Characters																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
**Perilampus hyalinus* group	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euperilampus scutellatus group	0	3	0	1	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1
Krombeinius megalaspis	1	2	0	?	?	?	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0
Krombeinius eumenidarum	0	2	0	1	0	1	1	0	0	1	2	0	0	0	0	1	0	0	1	0	0	1	0
Krombeinius saunion	0	2	0	?	?	?	1	0	0	1	2	0	0	0	0	0	0	1	0	1	0	1	0
Krombeinius taiwanensis	1	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	0
Krombeinius lerouxi	1	2	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Krombeinius srilanka	1	1	0	?	?	?	1	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0

same internodes on each of the cladograms. After further consideration it was obvious that a suite of morphological attributes is associated with a tendency towards either an elongation or a shortening of the mesosoma. The prepectus is fused to the pronotum and bridges the gap between the lateral pronotum and the mesopleuron. These three characters provide no unique information and are different ways of describing the same morphological relationship. The multiple manifestations of the pronotum/prepectus correlation had confounded the search for parsimonious cladograms and my solution was to code only a single character. This character is a multistate character with four states (Fig. 18). In the outgroup and in all species of *Perilampus,* the prepectus is broader than the adjacent pronotum (state 0). In all species of *Euperilampus* the prepectus is very narrow, less than one-fifth the width of the adjacent pronotum (state 3). Neither of these states are found in *Krombeinius*; the prepectus is intermediate in size. In *K. eumenidarum, saunion, lerouxi,* and *megalaspis* the pronotum is greater than one-third (about 0.4) the width of the pronotum (state 2). In *K. taiwanensis* and *K. srilanka* the prepectus is much wider, greater than one-half (about 0.6) the width of the adjacent pronotum (state 1). My initial approach was to code a linear transformation series from the broad prepectus of *Perilampus* to the narrow prepectus of *Euperilampus* (Fig. 18a). This transformation was inconsistent with the final tree (CI = 0.75). This character was then analyzed as unordered allowing any possible transformation to add only a single step to the tree. This procedure resulted in a single shortest tree with this character exhibiting no homoplasy; the suggested transformation series is presented in Figure 18b. The cladogram (Fig. 19) suggests a revised interpretation of the evolution of the prepectus in the Perilampidae. The most parsimonious interpretation is that the common ancestor of *Krombeinius* and *Euperilampus* had a narrow prepectus (state 3), that a broader prepectus is a groundplan character in *Krombeinius* (state 2), and a still broader prepectus (state 4), approaching in size the prepectus of *Perilampus* (state 0), is a synapomorphy of *K. taiwanensis* + *K. srilanka.*

Character 3. The axillula is developed as a fingerlike lobe in all members of the *Perilampus hyalinus* group and in species related to *Perilampus platigaster* Say (Smulyan, 1936). A similar axillula occurs in *K. taiwanensis* (Fig. 6). The axillula is much shorter in all other species groups of *Perilampus* (state 0) and in related perilampid genera and the fingerlike configuration is therefore regarded as derived (state 1). The PAUP parsimony program suggests that the common ancestor of *Euperilampus* + *Krombeinius* and the *Perilampus hyalinus* group had the fingerlike axillula and a reversal occurred in the common ancestor of *Euperilampus* + *Krombeinius.* An equally parsimonious interpretation has the derived state occurring independently in the *P. hyalinus* group and in *Krombeinius taiwanensis.* I favour the latter interpretation and this example indicates the uncertainty that can be caused by apomorphies in the outgroup.

Characters 4, 5, 6. Three characters were used to describe the transformation series for the labrum. The labrum of all species of *Perilampus* shares the same basic configuration (Domenichini, 1969, Pl III, figs. 4, 5; Darling, 1987). Distinct aboral setae are present and the labrum does not have a deep median excision; there is no central stalk (states 0, 0, 0). Three derived characters are present in *Krombeinius* and/or *Euperilampus*: aboral digits reduced, setae sessile (states 1, 0, 0; Fig. 4); labrum bilaterally symmetrical, with deep median excision (states 0, 1, 0; Darling, 1983b,

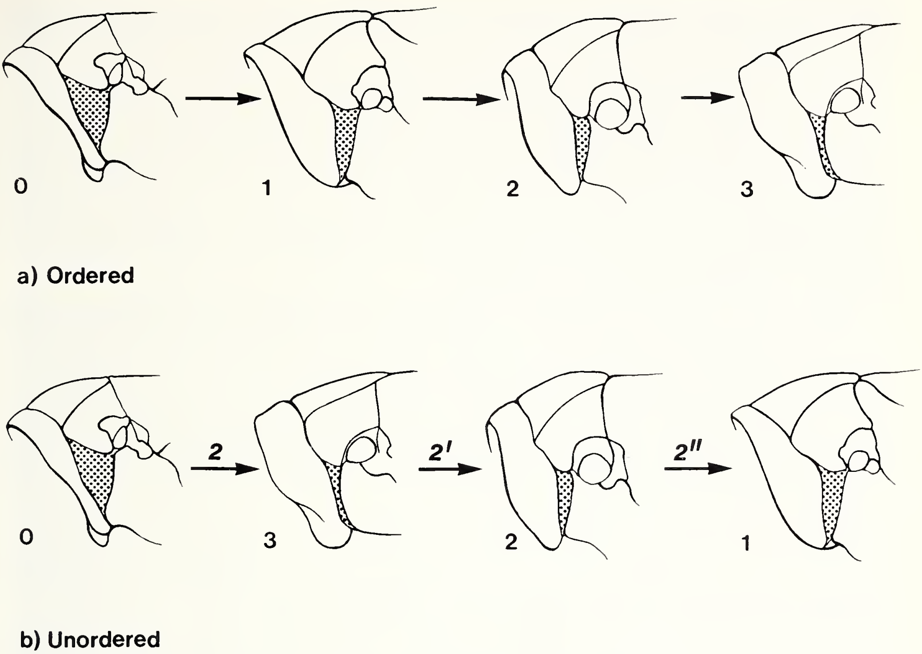


Fig. 18. Character states and possible transformation series for prepectus size (stippled), relative to width of adjacent pronotum (see "Phylogenetic Analysis," Character 2 in text).

fig. 3); labrum with a narrow central stalk, expanded distally with 7 or 8 short digits (states 0, 0, 1; Fig. 4).

Characters 7, 8. The third metasomal tergite is subequal in size to T2 in all species of *Perilampus* (states 0, 0). Specialization is judged to have resulted in two independent apomorphic states: T3 transverse, wider than long, much shorter than T2 along midline (states 0, 1; Darling, 1983b, frontispiece); T3 massive, as long as wide, longer than T2 along midline (states 1, 0; Darling, 1983b, fig. 1).

Character 9. As noted by Bouček (1978), the scutellum of *K. megalaspis* (fig. 2) is strongly convex in lateral view (state 1), a character shared with *K. taiwanensis* (Fig. 6). The scutellum is not strongly convex in lateral view, and tapers gradually towards the apex (state 0) in the outgroup, in *Euperilampus* and in all other species of *Krombeinius* (Fig. 13; Bouček, 1978, fig. 1; Darling, 1983a, fig. 1).

Character 10. The stigmal vein makes a 90° angle with the marginal vein (state 1) in *Krombeinius eumenidarum* and *K. saunion* (Darling, 1983a, fig. 1). The plesiomorphic state is an oblique angle (state 0) and is found in the outgroup, in *Euperilampus,* and in two species of *Krombeinius* (Rasplus, 1987, fig. 3). In *K. taiwanensis* the stigmal vein is coded as plesiomorphic, although the angle is somewhat intermediate (Fig. 8).

Character 11. In *Krombeinius eumenidarum* and *K. saunion* the lateral pronotum has a distinct callus suggesting bumpy shoulders (state 2; Bouček, 1978, fig. 1; Darling, 1983a, fig. 1). In the outgroup, *Euperilampus, K. megalaspis* (Bouček, 1978, fig. 2) and *K. srilanka* (Fig. 13) the pronotum is regularly convex (state 0). A morphologically intermediate condition occurs in *K. lerouxi* and *K. taiwanensis*; the lateral pronotum is convex with only a slight indication of a callus (state 1; Fig. 6).

Character 12. The prepectus of Perilampidae is foveate, with many foveae occurring in *Perilampus* (state 0; Darling, 1983b, figs. 60, 61). In *Euperilampus scutellatus* and *Krombeinius megalaspis* there is only a single dorsal fovea (state 1). Multiple foveae are found in all other species of *Krombeinius* (Fig. 7; see also Bouček, 1978, fig. 1; Darling, 1983a, fig. 1). Although this character may be influenced by the absolute width of the prepectus (character 2), single and multiple foveae occur in species with the same configuration of the prepectus.

Character 13. The propodeum is very short in *K. megalaspis,* subequal in length to the metanotum (state 1). In *Perilampus* and all other species of *Euperilampus* and *Krombeinius* the propodeum is about twice as long as the metanotum (state 0).

Character 14. Smooth areas with reduced sculpture or completely devoid of sculpture (state 0) are usually present along the notauli in the Perilampidae and are present in the *P. hyalinus* group (Darling, 1983b, fig. 60). The mesoscutum is evenly sculptured only in the *Euperilampus scutellatus* and *E. tanyglossa* species groups, and in *Krombeinius megalaspis* (state 1).

Character 15. The inner orbits are developed as massive scrobal walls in all species of *Euperilampus* (Darling, 1983b, figs. 4–9) and to a lesser degree in the *Perilampus hyalinus* group (e.g., *P. carolinensis* and *P. regalis*). The inner orbits are not so developed in the plesiomorphic species groups of *Perilampus* and in related genera (*Burksilampus, Steffanolampus*). The massive scrobes are therefore regarded as plesiomorphic (state 0) in *Euperilampus* and *Krombeinius.* Only *Krombeinius taiwanensis* has reduced scrobal walls (state 1), here regarded as a reversal to the plesiomorphic condition.

Characters 16, 17. Two characters were coded to represent the sculpture patterns found in the various species. The third metasomal tergite is completely smooth (states 0, 0) in the *P. hyalinus* group. Distinct, but small, punctures are present laterad, near the border of T2 and T3 in two species of *Krombeinius* (states 1, 0). This sclerite is almost completely sculptured in *K. srilanka* (states 0, 1).

Character 18. Distinct tentorial pits (state 1) are present in *K. saunion* (Darling, 1983a, fig. 16). In all other taxa the tentorial pits are indistinct (state 0, Fig. 1; Darling, 1983a, figs. 8, 12; Darling, 1983b, figs. 5, 10, 11, 38). [Note: weak tentorial pits are present in *Euperilampus aureicornis* but not in its sister species *E. tanyglossa*.]

Character 19. The propodeum has a distinct median ridge in the *Perilampus hyalinus* group (state 0; Darling, 1983b, fig. 63). In *Krombeinius eumenidarum* and in all species of *Euperilampus* the median area of the propodeum is foveate and lacks a complete median ridge (state 1; Darling, 1983b, figs. 17–20). My previous cladogram regarded the lack of a median ridge as a synapomorphy of *Krombeinius* + *Euperilampus* (character 14); only the type species, *K. eumenidarum* was included as an exemplar. This character exhibits considerable homoplasy and is here interpreted as a synapomorphy of *Euperilampus* and also as a convergent autapomorphy of both *Krombeinius eumenidarum* and *K. srilanka.*

Character 20. The scutellum is developed as an elongate spine (state 1) in *K. saunion* (Darling, 1983a, fig. 15). The scutellum is truncate (state 0) in all other species of *Krombeinius* (as in Figs. 5, 12), in all species of *Perilampus,* and in *Euperilampus* *scutellatus.* However, two species of *Euperilampus* (*E. gloriosus* and *E. spina*) have the scutellum produced as a prominent spine. These species are representatives of distinct species groups of *Euperilampus* (Darling, 1983b) and the spine-like scutella are also interpreted as non-homologous autapomorphies in these species.

Characters 21, 22. The relative length of the marginal vein is coded as two transformation series. The plesiomorphic state, found in *Perilampus hyalinus,* has the marginal vein longer than the postmarginal vein, but less than 1.5 times the length of the postmarginal vein (states 0, 0; Darling, 1983b, fig. 62). The marginal vein is very short in all species of *Euperilampus,* shorter than the postmarginal vein (states 1, 0; Bouček, 1978, fig. 6; Darling, 1983b, figs. 57–59). The marginal vein is slightly longer in most species of *Krombeinius,* marginal vein is between 1.5 and 2 times the length of the postmarginal vein (states 0, 1; Fig. 8; Darling, 1983a, fig. 1). The only exception is *K. srilanka* in which the marginal vein is only 1.35 the length of the postmarginal vein; here regarded as a reversal to the ancestral condition. Character 21 is an unequivocal synapomorphy for *Euperilampus.* However, character 22 is somewhat less certain. Homoplasy is present and the observed differences are subtle. This hypothesis will have to be tested when the species groups of *Perilampus* are considered in detail. In the final analysis both *Krombeinius* and *Perilampus* may be shown to have the plesiomorphic configuration of the marginal vein, an interpretation that would not affect the hypotheses of relationships (Fig. 19).

Character 23. The scutellum of all species of *Euperilampus* has a distinct crenulate marginal rim that is separated from the rest of the scutellum by a distinct carina (state 1; noted by Bouček, 1978, figs. 3–5, 7–11; Darling, 1983b, figs. 12–16, 34, 36, 37). The marginal rim is absent (state 0) in all species of *Perilampus* (Darling, 1983b, figs. 60, 61, 63, 66) and in *Krombeinius* (Fig. 5; Bouček, 1978, figs. 1, 2; Darling, 1983a, figs. 1, 7, 11, 15). The vaulted scutellum of *K. megalaspis* and *K. taiwanensis* (character 10) could be considered as a possible morphological intermediate to the marginal rim of *Euperilampus.* All that would be necessary is to delimit the apex of the scutellum with a complete carina. This, however, does not appear to be the case. If characters 10 and 23 are coded as a single linear transformation series with the vaulted scutellum as intermediate, additional steps would be added to the final cladogram. In addition, the scutellum of *K. srilanka* is most similar to species of *Euperilampus* (see description for details), and this species does not have a vaulted scutellum (Fig. 13).

Discussion. Figure 19 is the most parsimonious cladogram for the 23 characters (length = 36, consistency index with autapomorphies removed = 0.667); there are no other equally parsimonious trees. Trees slightly longer than the shortest possible tree were also evaluated for topology, in particular, monophyly of the recognized genera. There are 13 trees with length 37 of which 11 support monophyly of the genera. The strict consensus tree for these 14 trees is almost completely unresolved, only supporting the monophyly of the ingroup and the sister group relationship of *K. eumenidarum* + *K. saunion.* As discussed above, character 10 is somewhat tenuous. When this character is deleted there are 20 equally parsimonious trees (length = 35) and the consensus tree only recognizes the monophyly of *Euperilampus* + *Krombeinius.* The cladistic relationships for the species of *Krombeinius* are not robust and would be expected to change if additional taxa or characters were added to the analysis. In fact, two of the species were incorporated into the study after initial

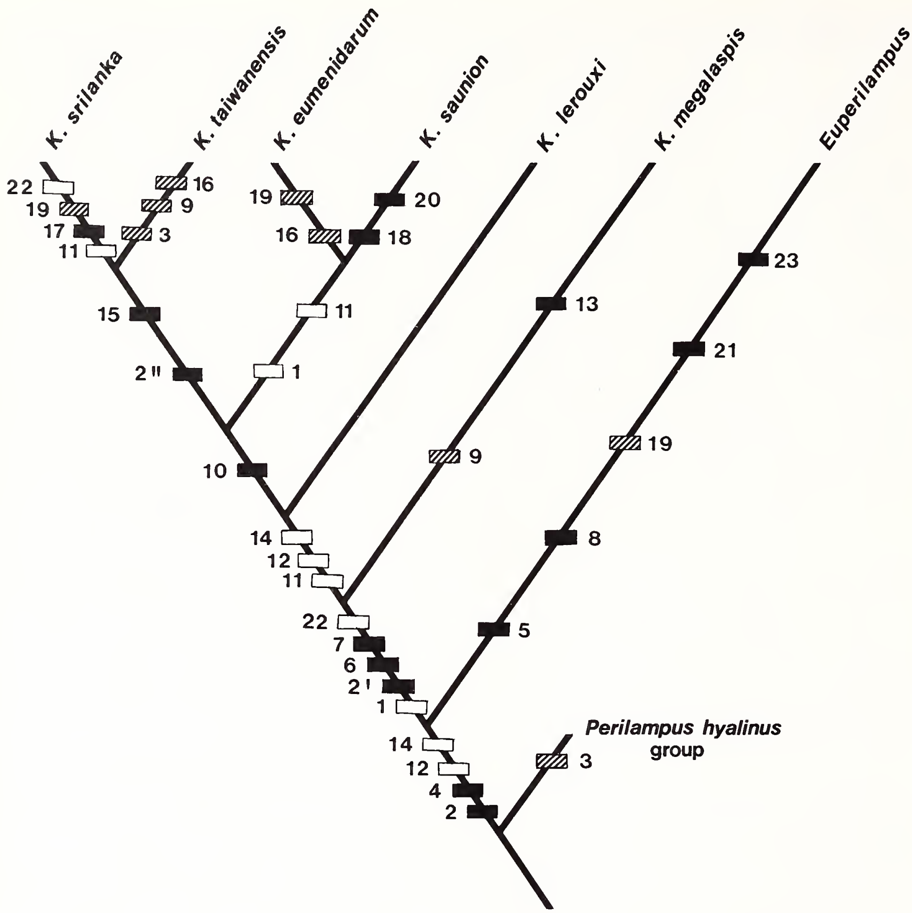


Fig. 19. Most parsimonious cladogram for data matrix in Table 1 (see text for discussion of character polarity and coding). Numbers refer to characters discussed in text and solid bars (■) indicate unique and unreversed apomorphies, and dashed bars (▨) indicate convergent apomorphies and open bars (□) indicate characters with reversals. The subsequent transformations of character 2 are indicated as 2′ and 2″.

analyses were completed (*K. lerouxi* and *K. srilanka*) and this did result in altered degrees of relationships.

A persistent source of confusion in cladistic analysis is the treatment of multistate characters. The use of the unordered algorithm of the PAUP program to interpret the evolution of pronotum shape suggests that considerable care should be exercised in the coding of multistate characters. The effect of coding transformation series as single linear sequences should be evaluated by comparison with alternative codings or by unordering the states. In many data sets homoplasy introduced by coding single intuitive transformation series results in multiple equally parsimonious trees which differ in topology. This problem is much more prevalent in data sets with low consistency indices. If classifications and binominal nomenclature are to be inexorably tied to cladistic analyses then considerable attention should be given to the assessment of not only equally parsimonious trees but also to slightly longer trees. Care should also be used in coding multistate characters.

In summary, the monophyly of *Krombeinius* is strongly supported by this analysis, as is the monophyly of *Euperilampus* and the sister group relationship of these genera. This analysis is also satisfying in that characters that should intuitively have a high weight, in particular complex, unique and unreversed morphological features (e.g., characters 2, 4, 6, 7, 8), support the major branch points, and characters that would be judged a priori to be evolutionarily labile, such as surface sculpture (e.g., characters 14, 16, 17) are interpreted as convergent similarities of terminal taxa.

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